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THE SCALES OF FRESHWATER FISHES.

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Professor N. S. Shaler,¹ writing of his experiences as a student under Agassiz, said: "I acquired a considerable knowledge of the literature of ichthyology, becoming especially interested in the system of classification, then most imperfect. I tried to follow Agassiz's scheme of division into the order of ctenoids and ganoids, with the result that I found one of my species of side-swimmers had cycloid scales on one side, and ctenoid on the other. This not only shocked my sense of the value of classification in a way that permitted of no full recovery of my original respect for the process, but for a time shook my confidence in my master's knowledge."

I quote this, because the breakdown of Agassiz's original system of classification by scales affected not only Professor Shaler, but many others, to the detriment of lepidology. Dr. Jordan, in his great work, "A Guide to the Study of Fishes" (1905), devotes only two pages to the discussion of scales, with a couple of figures. In the descriptions of fishes published by various authors, much is made of the number and size of the scales, but little of their structure, and it rarely happens that an ichthyologist even takes the trouble to remove a scale from the fish he is studying, in order to determine its characters. These remarks apply especially to the teleosts—the ordinary fishes of modern times, and it is of course true that students of the "ganoids" and their allies, mostly fossil, have never neglected the scales. The ganoids have greatly thickened scales, usually rhombic in form, which are well preserved in the rocks; as Agassiz so well insisted, they afford a most important aid to the classification of these animals, particularly in the numerous cases in which the skeleton is poorly preserved. Recent researches, while destructive to certain theories which Agassiz considered im-

¹ *Atlantic Monthly*, February, 1909, p. 222.

portant, have only emphasized his doctrine that the scale is of great taxonomic value. I have paid little attention to the ganoids and their relatives, and will not attempt to discuss them, here, but may call attention to the important memoir by Goodrich¹ in which it is shown that the so-called ganoid scales can be divided into three very distinct groups, called the cosmoid, palæoniscoid ganoid and lepidosteoid ganoid. Mr. Goodrich, having distinctly differentiated these types, applies his work to the classification of some difficult forms, with striking results.

Teleostean scales, the ordinary imbricated readily removable scales of fishes, were classified by Agassiz as cycloid and ctenoid, and his names are still in current use. The cycloid scale is one in which the apical margin is what a botanist would call entire, that is without teeth or serrations. The ctenoid or comb-like scale has the margin dentate, serrate or spiny. It is now well-known that these are not fundamental divisions, some families having both ctenoid and cycloid types, and as Shaler has stated, it is possible for both kinds to exist on a single flat-fish. Nevertheless, the distinction is usually an important one, while the scales have innumerable other characters of value, not used in Agassiz's system of classification.

My own work with fish-scales had what might be called an accidental beginning. In the course of class-work, my students and I took occasion to examine the scales of the fresh-water fishes of Colorado. We soon perceived that they had excellent distinctive characters, and thereupon sought literature on the subject. Failing to find anything satisfactory, we wrote to Dr. D. S. Jordan, who promptly gave us the desired information, or rather, indicated the lack of it. Girard, in his report on the fishes of the Mexican Boundary Survey, had given numerous figures of the scales of fresh-water fishes, but had not discussed or classified them. About fifty years ago it appears that it was seriously intended to work up the lepidology of the American teleosts, but for some reason nothing came of it, beyond the publication of the figures mentioned. Later, Dr. Boulenger gave me access to the work of Fatio (1882), in which the scales of all the fishes of Switzerland are figured; also to the great work of

¹ *Proc. Zool. Soc. London*, 1907, pp. 751-774.

Sauvage on the fishes of Madagascar, containing numerous figures of scales of Acanthopterygian fishes. In other writings, here and there, are various figures of scales, usually with little discussion. The scales of *Gadus* (codfish and allies) have been beautifully figured and fully discussed by Dr. H. W. M. Tims (1905).¹

Dr. Jordan, with great kindness, sent me a fine series of freshwater fishes from the collections of Stanford University, while Dr. Evermann was equally good in supplying numerous species from the Bureau of Fisheries. I thus obtained nearly all of the principal forms of North American Cyprinidæ or carp-like fishes. The following summer I visited the British Museum, and was indebted to Dr. Boulenger for the opportunity of investigating the scales of nearly all the principal old-world cyprinids, and a like series of African characinids. I also obtained through him many African fishes of other families. Quite recently I have received from Dr. Eigenmann, of the University of Indiana, an extremely fine series of South American characinids. With all these, and some others, it has been possible to test rather thoroughly the value of scale-characters, and the result has been to show that while they are not rarely deceptive, through convergence, they are on the whole of great taxonomic importance. As in most other taxonomic work, there are disturbing elements due to individual variability and differences of age, but while these are sure to lead to various minor errors, they will not much affect the broader results. The key to the origin of the sculpture of a teleostean scale is apparently to be found in that ancient type the bowfin of North America, *Amia calva*. Fig. 1 shows part of the base of a scale of this fish, which it will be observed consists of longitudinal strands or fibres, separable elements which fray out basally.² In the apical field these are directed toward a broad rough nuclear area. A close approximation to this is found in a very old type of teleosteans, the lady-fish, *Albula*. In this, however, appear also the beginnings of the radial lines, extending from the nucleus of the scale to the margin. As we go higher

¹ Dr. B. L. Chaudhuri informs me that Dr. John McClelland published an account of the scales of Indian Cyprinidæ in the appendix to his work on these fishes, in 1839. This I have not seen.

² See Smithsonian Misc. Coll., Vol. 56, No. 3, p. 2, 1910.

in the scale of fish-evolution, these radiating lines or *radii* often become very prominent, while the longitudinal strands usually become united above and below, forming circular fibers which we have designated *circuli*. The nomenclature of these structures was based on a normal highly-developed scale, in which the *circuli* deserved their name, and since then the term has been applied to the same elements wherever found, so that I have had to refer, rather illogically, to *longitudinal circuli*. Perhaps it would be better to call them fibrillæ.

On looking at a normal scale, in which the *circuli* are strictly circular, it would be natural to regard them as lines of growth, like those on a snail's shell. There are real lines of growth, however, and these do not necessarily coincide with or have anything to do with the *circuli*.

In the salmon and trout (*Salmo*) the scales are strictly cycloid, and have only *circuli*. Fig. 2 shows a scale of the bluefin, *Argyrosomus nigripinnis*, a member of the salmon family. This shows a marked deviation from the simple *Salmo* type, in that there are distinct laterobasal angles, the *circuli* of the apical field are less dense than those of the basal, and there are slight indications of apical *radii*. It is no very great step from this to the scale of *Moxostoma aureolum*, one of the suckers (Fig. 3), but it will be noted that in the sucker, as indeed in all members of the Catostomidæ so far examined, there are very distinct basal *radii*. In the typical suckers, *Catostomus*, the scale is oval, not unlike that of *Salmo* in shape, and there are *radii* all around. This is well shown in Fig. 4, *Pantosteus santa-anæ*, from California. The possession of basal *radii* separates the Catostomidæ from the great majority of American cyprinids, although a few genera of the latter family have them, notably *Chrosomus* (Fig. 5, *C. dakotensis*), the scale of which closely resembles that of *Pantosteus* in sculpture, though differing in shape. Among the old world cyprinids (carp family) basal *radii* are very common, and it is curious that the common European minnow (*Phoxinus phoxinus*) has scales of quite the same type as the American *Chrosomus*. There is reason to believe that the suckers are an ancient family, close to the old stem from which the carp family arose. They are nearly confined to North America, though spar-

ingly represented in eastern Asia. From this circumstance one might look for the earliest types of Cyprinidæ also in America, but the strong indications are that they are old-world forms, the modern American cyprinids, with a few possible exceptions, having arrived in comparatively recent times from Asia. Nevertheless, the carp family in this country must be only of comparatively, not actually, recent origin, since it has had time to develop innumerable species, and a considerable series of endemic genera. The distinctness of the American Cyprinid fauna has indeed been emphasized by the scale work, it being shown that the so-called *Leuciscus*, *Rutilus*, etc., of America are not congeneric with the European fishes bearing these names. It is probable, in fact, that all of the American Cyprinidæ are generically distinct from those of Asia and Europe.

Returning again to the bluefin scale, we can take a new point of departure in Fig. 6, the Asiatic cyprinid *Squaliobarbus curriculus*. Here the general form remains the same, except for a moderate elongation, the apical circuli become more widely spaced, the apical radii are evident, but there are no basal radii. A European scale of nearly the same type is that of *Leuciscus illyricus* (Fig. 7). In other cases, the scale may be more parallel-sided, with a broad truncate base, as is shown in the Asiatic *Labeo sladoni* (Fig. 8) and *Rhinogobio typus* (Fig. 9).

In order to illustrate the value of scale characters within a limited group, I give a series of figures of species usually referred to *Leuciscus*, the dace and its allies. *Leuciscus rutilus* (Fig. 10) and *L. friesii* (Fig. 11) are European; *L. hakuensis* (Fig. 12) and *L. jouyi* (Fig. 13) are Japanese. The remaining four are North American, and because of their very different scales, and other reasons, I have removed them to another genus, *Richardsonius* Girard. *R. orcutti* from California (Fig. 14) constitutes a distinct subgenus, the scale having basal radii. *R. pulchellus* (Fig. 15) is of the Rocky Mountains. *R. carletoni* (Fig. 16) is a distinct type from Maine, while *R. thermophilus* (Fig. 17) inhabits warm springs in Oregon. It will be observed that in the European forms the large scales have exceedingly fine circuli. In the American, the scales are very much smaller, and the circuli are very coarse and widely-spaced. This is in general a charac-

teristic distinction between New World and Old World Cyprinids, although some of the Old-World genera have widely-spaced circuli. The two Japanese species, as one might expect, are rather intermediate between the European and American. They probably should constitute a new subgenus or genus. *Leuciscus illyricus* (Fig. 7) has widely spaced apical circuli, and therein departs in the direction of the Japanese and American fishes.

The Characinidæ are a large family of freshwater fishes occurring in the Ethiopian and Neotropical regions, but not elsewhere, with the exception of a few which enter the Palæarctic in the Nile Valley and the Nearctic in southern North America. This curious distribution has naturally aroused interest among naturalists, and while it is probable that America was their original home, it is a question whether they reached Africa across what is now the Atlantic, or once inhabited the north and passed southward into the Ethiopian area. I should think the latter supposition more probable, but for the fact that as yet we have no trace of fossil characinids outside of their present area. The characinids belong to the same general group as the cyprinids, but are unquestionably more primitive, in spite of the fact that many of their members are exceedingly specialized in certain particulars. Among the African characinids is a group, the Alestini, having a very characteristic type of scale.¹ This, which I call the alestiform scale, is more or less hemispherical in outline, cycloid as to the margin, with a few very strong radii. It seems to be an old type, because we find it nearly repeated in certain of the relatively primitive families, as for instance the Phractolæmidæ (*Phractolæmus ansorgii*, Fig. 17a), a rare type from the Niger and Congo rivers. The *Phractolæmus* scale, however, is incipiently ctenoid. A different scale, yet of the general alestiform type, is found in *Pantodon buchholzi* (Fig. 18), another rare and isolated genus from the Niger and the Congo. On this fish the circuli have a peculiar and very characteristic bead-like appearance. Passing to the more specialized cyprinids, we find the alestiform scale not uncommon, and a good example from an Asiatic fish (*Barbus mahecola*, Fig. 19) is given. It will also be noted that *Leuciscus rutilus* of Europe (Fig. 10) has much the

¹ See Smiths. Misc. Coll., Vol. 56, No. 1, plate 1, figs. 4, 5, 6.

same sort of scales though lacking the characteristic lateral radii of the Alestini and the *Barbus*.

In some of the cyprinid alestiform scales the nuclear region is broken up into polygonal areas, but in the curious African Mormyridæ¹ there is a characteristic system of anastomosing radii, forming a network. This is unique, so far as material seen by me shows, except for the case of *Heterotis niloticus* (Fig. 20), a member of the ancient and now much reduced family Osteoglossidæ. In this fish, which inhabits tropical Africa north of the Equator, the network is extremely well developed.²

An extremely distinct and interesting type of scale is found in the tench of Europe, *Tinca vulgaris* (Fig. 21). This seems to be a relatively old type, formerly more abundant. Through the kindness of Dr. A. S. Woodward, of the British Museum, I was able to examine the miocene fossil species *Tinca furcata* of Agassiz, and the nominal but apparently synonymous *T. magna* of Winkler, and found the scales to be wholly characteristic of the genus. It is a singular thing that in North America there exists a fish called *Algansea tincella*,—named *tincella* by Valenciennes because of its resemblance to a tench,—which has scales of the same general type though not so extreme. Mr. Regan has described two other species of the genus *Algansea*, *A. affinis* and *A. stigmatura*, and he informs me that they have scales like those of *tincella*.

On the other hand, there are scales which so far as shape goes resemble those of *Tinca*, and yet offer marked differences in the details of the sculpture. Such is the scale of the Asiatic *Schizothorax biddulphii* of Gunther (Fig. 22). Among the American cyprinids, especially the smaller forms commonly known as minnows, there are many scales which at first sight look alike. In some cases, there is actually no definable difference, but often sufficient familiarity with the scales enables one to recognize them without difficulty. I illustrate a series of such forms, *Lavinia exilicauda* (Fig. 23), *Phenacobius mirabilis* (Fig. 24), *Notropis galacturus* (Fig. 25) and *Pimephales anuli* (Fig. 26); also a similar European scale, *Gobio fluviatilis* (Fig. 27). In all

¹Smiths. Misc. Coll., Vol. 56, No. 3, p. 2, figs. 1, 2.

²Since this was written I have determined that all the Osteoglossidæ, and also all living Dipnoans (lung-fishes) have the radial network.

these scales there is much variation, which is at times confusing, although it usually does not affect the fundamental character of the pattern. Thus I described the scale of *Chondrostoma soëtta*, from Italy, as having few apical radii, distinguishing it thus from certain Spanish species. Noting later that this did not agree well with Fatio's figure, I asked Mr. Regan to look into the matter and he found that on the same fish immediately adjacent scales had many and few radii respectively. Consequently my diagnostic character proves of no value, but it will be noted that the variation affects the development rather than the character of the markings. Greater differences are noted when the scales are taken for different parts of the body, and for purposes of comparison I always take them from near the middle of the side, close to the lateral line. Fig. 28 and 29 show an extreme case, that of the curious little fish *Ericymba buccata*, from Indiana. Fig. 28 is a normal scale, and Fig. 29 is from the subdorsal region about 5 mm. in front of the dorsal fin. These two scales are from the same fish.

Occasionally very marked abnormalities occur. Thus on a specimen of *Ostebrama feæ* I found a greatly enlarged scale on the middle of the side, below the lateral line. It was about 8.5 mm. long, six times as long as the exposed parts of the normal scales, but not differing essentially in sculpture. The age of the fish is also often of importance. Fig. 30 shows a scale of *Gila robusta* from Arizona. It was taken from a young fish, and for some time I did not know that the adult scales of *Gila* have a characteristic basal lobe, as indeed was figured long ago by Girard in the report of the Mexican Boundary Survey.

There is an interesting case outstanding, in which the value of scale characters for the separation of very closely allied fishes has yet to be determined. From Stanford University I received a number of specimens of *Myloleucus symmetricus*, collected in different localities. These were sent principally because Dr. J. O. Snyder had already noticed the variability of this fish in other than scale characters, and it was suspected that it might include some separable forms. A study of the scales revealed four apparently distinct types. (1) Scale broad, small. Navarro River, Gualala River (California) and north to Drew Creek in

Oregon. (2) Scale broad, large. Napa River (California). (3) Scale oblong, more weakly sculptured. Ukiah Creek; Russian River (California). (4) Scale oblong, strongly sculptured. Conchilla Creek (California).

It appears from this that there is a broad-scaled form to the north coming south as far as Gualala River. From this it is only a few miles to Russian River, where the fish is oblong-scaled. Passing beyond, however, we find another broad-scaled variety in Napa River. It is suggested that the broad-scaled fishes, when in competition with the oblong-scaled, may get the better of them, and that the Napa River fish represents an invasion from the north away from the coast. All this, however, is at present based on far too little evidence, and is given here partly as an example of the kind of problem the scale-work brings up, and partly in the hope that someone will make an exhaustive study of the matter. Up to the present, I have not been able to get any further information, beyond what is given by Dr. Snyder in Bull. Bureau of Fisheries, XXVII, p. 175. In general, Dr. Snyder's results, based on other than scale characters, agree with mine, but he finds no difference between the fishes of Russian and Napa Rivers. No less than five specific names have been given to *M. symmetricus* as now understood; probably two or three of these will be available for the necessary segregates. While most fish scales fall readily into a systematic arrangement, we occasionally meet with one which differs greatly from any other known to us. Such is the scale of *Kneria cameronensis* Boulenger (Fig. 31), a small fish belonging to a peculiar family found only in tropical Africa. In this the radii run from one end of the scale to the other and the circuli are for the most part broken up into peculiar marks between them.

The study of fish-scales opens up a vast new field, the scales of most of the common fishes being still undescribed. Fish scales also may claim our attention for their beauty as microscopical objects. Their preparation involves no difficulty; they are best mounted dry between thin microscopical slides; or when small, they may be mounted on a slide under a cover glass. At first, I placed them in balsam, but this greatly obscures the markings, and is altogether undesirable.

For the means of obtaining the photographic figures (the work of Mr. T. C. Black) I am indebted to a grant from the American Association for the Advancement of Science. The drawings are by Miss Evelyn V. Moore. In this paper I have described and figured only scales of fresh-water species. At some future time, it may be possible to give a similar account of the marine families, and of several fresh-water groups now omitted.

EXPLANATION OF PLATE I.

FIG. 1. *Amia calva*. Plymouth, Indiana. Dr. Evermann.

FIG. 2. *Argyrosomus nigripinnis*. Dr. Graenicher.

FIG. 3. *Moxostoma aureolum*. Dr. Graenicher.

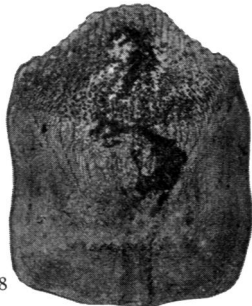
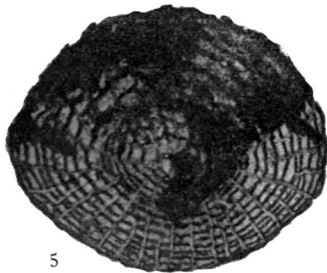
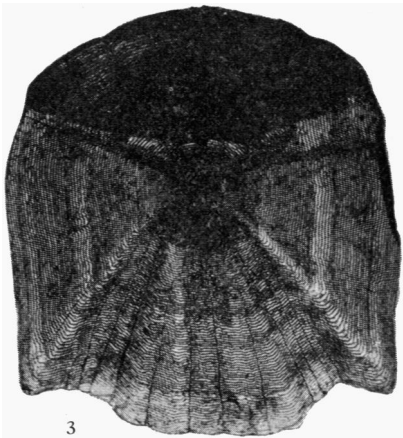
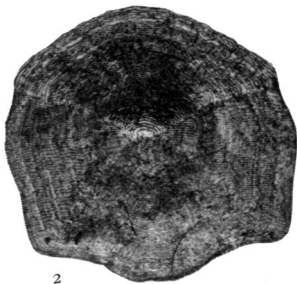
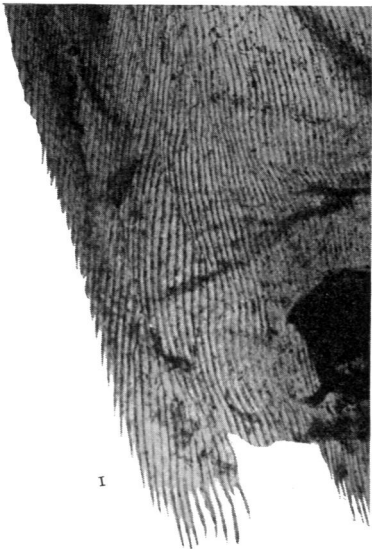
FIG. 4. *Pantosteus santa-anæ*. Santa Ana River, California. Stanford University.

FIG. 5. *Chrosomus dakotensis*. Valentine, Nebraska. Bureau of Fisheries.

FIG. 6. *Squaliobarbus curriculus*. Mountain stream near Kiu-Kiang (Styan). British Museum.

FIG. 7. *Leuciscus illyricus*. R. Tadro, Dalmatia (Dr. Werner). Brit. Museum.

FIG. 8. *Labeo sladoni*. Mandalay (F. Day). Brit. Museum.



EXPLANATION OF PLATE II.

FIG. 9. *Rhinogobio typus*. Kiu-Kiang (Styan). Brit. Museum.

FIG. 10. *Leuciscus rutilus*. Salisbury, England (Odgen Smith). Brit. Museum.

FIG. 11. *Leuciscus friesii* = *L. meidingeri*. Lake of Derkos, Constantinople. Brit. Museum.

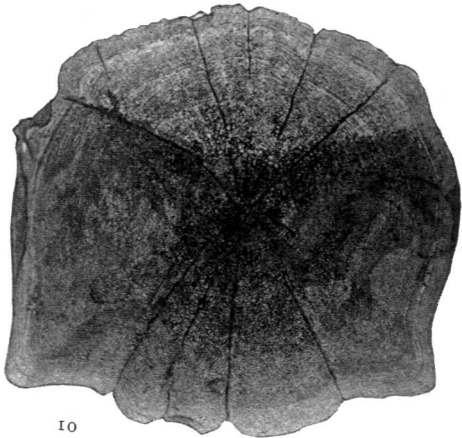
FIG. 12. *Leuciscus hakuensis*. Yamada, Japan (R. Gordon Smith). Brit. Museum.

FIG. 13. *Leuciscus jouyi*. Sasuma, Japan (Anderson). Brit. Museum.

FIG. 14. *Richardsonius* (*Temeculina*) *orcutti*. Santa Ana River, California. Stanford University.



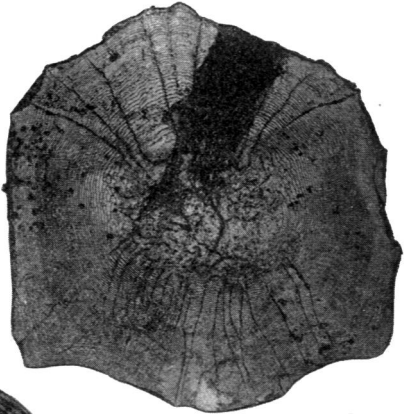
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EXPLANATION OF PLATE III.

FIG. 15. *Richardsonius (Tiogma) pulchellus*. Alamosa, Colorado. Stanford University.

FIG. 16. *Richardsonius (Cheonda) carletoni*. Cross Lake Thoroughfare, Maine. Bureau of Fisheries.

FIG. 17. *Richardsonius thermophilus*. Warm Spring, Harney Co., Oregon. Stanford University.

FIG. 17a. *Phractolaemus ansorgii*. Brit. Museum.

FIG. 18. *Pantodon buchholzi*. Brit. Museum.

FIG. 19. *Barbus mahecola*. S. Canara (F. Day). Brit. Museum.

FIG. 20. *Heterotis niloticus*. Brit. Museum.



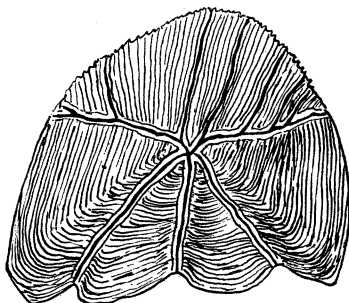
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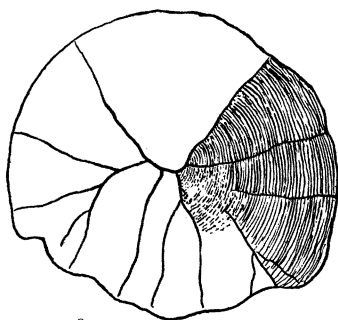
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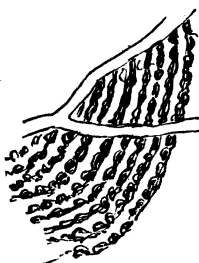
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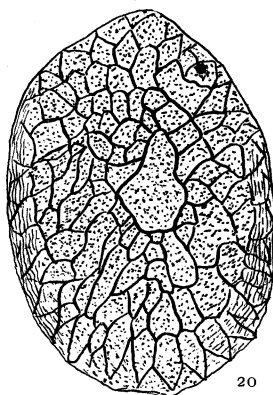
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EXPLANATION OF PLATE IV.

- FIG. 21. *Tinca vulgaris*. Constantinople. Brit. Museum.
FIG. 22. *Schizothorax biddulphii*. Lake Balyk-ky near Nijo. (St. Petersburg Mus.) Brit. Museum.
FIG. 23. *Lavinia exilicauda*. Coyote Creek, California. Stanford University.
FIG. 24. *Phenacobius mirabilis*. Bureau of Fisheries.
FIG. 25. *Notropis galacturus*. Saltville, Virginia. Bureau of Fisheries.



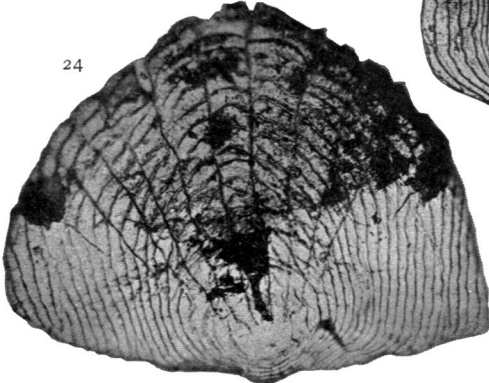
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EXPLANATION OF PLATE V.

FIG. 26. *Pimephales anuli*. Lunkasoos Lake, Maine. Bureau of Fisheries. (Note straight edge of skin across middle of scale.)

FIG. 27. *Gobio fluviatilis* (*G. vulgaris*). R. Neckar near Canstatt (Stuttgart coll.) Brit. Museum.

FIG. 28. *Ericymba buccata*. Wild Cat Creek, Indiana. Bureau of Fisheries. Figure reversed.

FIG. 29. *Ericymba buccata*. Wild Cat Creek, Indiana. From subdorsal region, in front of dorsal fin.

FIG. 30. *Gila robusta*. Tempe, Arizona. Stanford University.

FIG. 31. *Kneria cameronensis*. Brit. Museum.

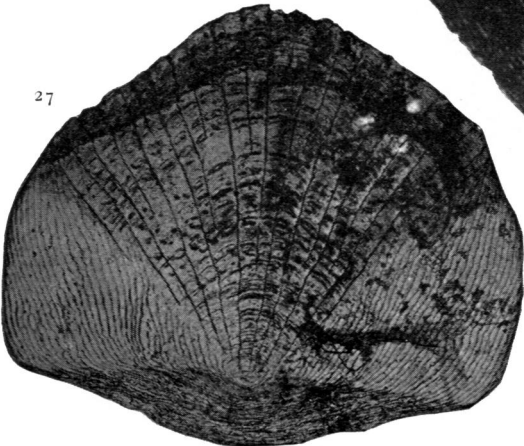
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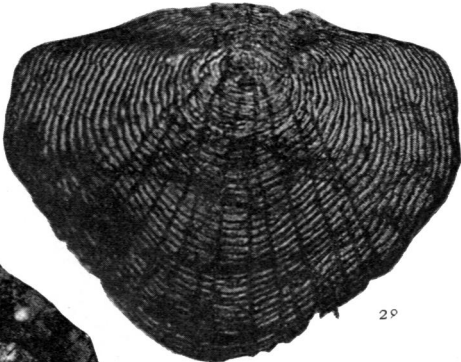
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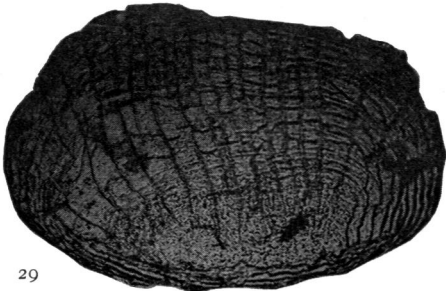
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